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GEOGRAPHICAL DISTRIBUTION OF THE BATS IN THE AUSTRALASIAN ARCHIPELAGO

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INTRODUCTION

The geographical distribution of the bats of the Indo-Australian region is a subject little touched upon in zoogeographical literature. It was treated to a limited extent by Andersen (1912) in his monumental systematic study of the Megachiroptera. But no broad treatment of the Microchiroptera from the geographical standpoint has yet been undertaken. Study of Mayr's (1944a) recent paper on Wallace's Line together with that of Raven (1935) and the critique by Brongersma (1936) has in part prompted the present examination of the distribution of the Chiroptera in Indo-Australia. In addition, my recently completed series of systematic studies on those mammals (Tate, 1939–1943)[1] has led me to undertake the present necessarily subjective study of chiropteran distribution in the Far East.

The 124 units listed in table 1 upon which subsequent discussion is based are those large, sharply distinct entities commonly accepted as "very distinct species." Included as single items are "species groups," the status of whose members has been variously recognized either as full species or as subspecies, according to the varying viewpoints of authors. "Pairs" and "representative species" are also included as single items. Groups of genetically distinct species that are somatically still scarcely differentiated have probably been included under single heads. All forms or geographical races that belong with reasonable certainty to one single species are merged into a single item. In short, the attempt is here made to draw conclusions from the geographical ranges of "good" species of bats only. A few small genera have been handled as single items.

The present work differs considerably from that of Raven (*ibid.*, pp. 183–185, 224–235), in the first part of which distribution by whole genera was shown, and in the second a complete list of 368 named forms, including species, subspecies, and synonyms. Thus, geographical races were given equal weight with full species. Besides, a number of synonyms can be detected.[2] Furthermore, in the expository portion of Raven's paper the bats are dismissed, rightly or wrongly, with half a dozen lines (p. 182).

Ever since Alfred Russel Wallace (1860, 1880) drew attention to the sharp faunal breaks that existed in the neighborhood of Wallace's Line, attempts have been made to explain such phenomena. Some writers, even though unable to explain them, have persistently urged their importance. Others, taking the opposite position, have denied the existence of any substantial barrier and asserted that in terms of geographical range, each single species was a law to itself. For some time, a considerable proportion of the zoological literature published upon "Wallacea," the group of islands between Asia and Australia, was influenced by the old Wallace's Line fetish, if only because many large groups of Asi-

[1] Four species indicated by me four years ago (Tate, 1942a) as somewhat isolated in position, namely, *Pipistrellus regulus* (p. 241), *Pipistrellus tasmaniensis* (p. 250), *Scoteinus rüppellii* (p. 281), and *Scoteinus orion* (p. 282), have recently been selected by Troughton ["Furred animals of Australia," second (revised) edition, 1943, pp. 349–355] as types of new genera, respectively named by him *Registrellus*, *Falsistrellus*, *Scoteanax*, and *Scotorepens*.

[2] Certain inaccuracies in Raven's generic list are here pointed out: *Nycteris* = *Petalia* (p. 184); *Coelops* = *Chilophylla* (p. 184); *Scotophilus* = *Pachyotus* (p. 185); "*Vespertilio*" may mean either *Myotis* or *Pipistrellus* (p. 185).

atic organisms that reached Java, Bali, and Borneo appeared to stop at the Mindoro, Macassar, and Lombok straits. It is now realized that many more species transgress Wallace's Line than the early writers supposed, as shown, for example, by Stresemann (1939, many distribution maps of birds), and that the extent of their transgressions is extraordinarily varied.

Wallace's Line, originally passing eastward south of the Philippines, was modified by Huxley (1868) to run between Palawan and Mindoro Islands, chiefly on the basis of the distribution of the brush turkeys or megapodes. All lands that lay to the south of Huxley's Line marking the northern limit of megapodes he called "Austral Asia," a term since used with varying significance. Huxley had no realization that he was also indicating much of the margin of the Asiatic continental shelf during the Pleistocene glacial periods.

Weber's Line, named by Pelseneer (1904), corresponded only in its southern part with the Australian continental shelf. North of Australia it ran through the deeps of the Banda Sea and the Molucca Strait, separating Celebes and Sula on the west from the northern Moluccas and Buru on the east; in the Lesser Sundas arc it passed between Timor and Sermata on the west and Babar with Tenimber (Timor Laut) on the east. The true margin of the Australian continental shelf passes east of Timor Laut and Kei and Ceram, as shown by Merrill (1926, map facing p. 1155), and De Beaufort (1926, map facing p. 202). A number of mammals have crossed the deep water from New Guinea to the Moluccas. The modified Weber's Line of Merrill, not that of Pelseneer, will be referred to in the present study.

The consensus of most writers (Mayr, *ibid.;* Scrivenor *et al.*, 1943; Rensch, 1936; Merrill, *ibid.*) is that the groups of islands lying between the Asiatic and Australian continental shelves of Pleistocene glacial times constitute an intermediate area that, besides having old endemic faunal and floral elements, gradually received substantial additions from both those areas in comparatively recent times, the Asiatic element as a rule being much larger than the Australian.

In the present paper the Chiroptera have been examined with a view to determining the number of local bat faunas that can be recognized; the extent of isolation of species and the number of endemics, and the relative ability of bats to cross those barriers that normally affect organisms of other kinds; the position, for the Chiroptera, of Mayr's "line of 50:50 balance"; and the meanings of Wallace's and Weber's Lines.

From a world viewpoint two ill-defined major distributional categories may be noted among the Australasian bats. The first category comprises genera of extremely wide geographical range, often extending to remote areas like western India, Africa, Madagascar, and, rarely, even America. Such are *Rousettus*, *Pteropus*, the *Cynopterus* group of genera, the Macroglossinae, *Myotis*, *Pipistrellus* and allies, *Chalinolobus* with the African genus *Glauconycteris*, *Eptesicus*, *Scoteinus*, *Scotophilus*, *Miniopterus*, the Kerivoulinae, the Molossidae, *Emballonura* with one related species in Madagascar and the genus *Coleura* in Africa, *Taphozous*, the Megadermidae, *Nycteris*, *Rhinolophus*, and *Hipposideros*.

The second category includes specialized genera and some special sections of the first category that have their principal centers of distribution among the islands or on the Australian continent east of the Asiatic continental shelf, with only occasionally mainland representatives. It comprises the markedly distinct megachiropteran genera *Dobsonia*, *Nyctimene*, *Macroglossus*, and derived groups, and *Notopteris*, as well as a large number of generic offshoots and sharply differentiated species groups, descended both from ancestors of the first-mentioned groups of widespread genera and families and from the Microchiroptera found to be indigenous or nearly so to the areas east of the Asiatic continental shelf. *Boneia* of Celebes is a specialized derivative of a *Rousettus*-like ancestor. *Pteropus* contains no fewer than 11 well-defined species groups native to the region, and two other groups, *P. hypomelanus* and *P. vampyrus*, extend to the continent. On

the other hand four isolated groups, according to Andersen (1912), occur in Madagascar. More widely separated from *Pteropus* are five species found only east of Wallace's Line, generically located under the three names *Acerodon*, *Pteralopex*, and *Styloctenium*. The macroglossine bats show a somewhat similar pattern. Four of the macroglossine genera occur only east of the "Line," though *Macroglossus* itself is found from Malaysia to Australia, and the Malaysian *Eonycteris* is represented in Celebes and the Philippines. In the suborder Microchiroptera development of strongly marked genera or species east of the limits of continental (including Sundaland) Asia is much less common. No example of it exists in the widespread genus *Myotis*. Of the eight groups of the equally dispersed *Pipistrellus*, present in the Asia-Australia region only three, *P. minahassae*, *P. tasmaniensis*, and *P. regulus*, are native to Wallacea or Australia. *Philetor* and the local Australian divisions of *Eptesicus* and *Scoteinus*, *Miniopterus tristis* and *M. australis*, come into this category. *Anamygdon* of the Solomon Islands appears to be an aberrant kerivouline. The Australian genus *Nyctophilus* is related only to *Antrozous* of western North America. *Mormopterus*, if Peters' (1881) views are still valid, has also American affinities. In *Emballonura*, considerable speciation has occurred in New Guinea and nearby. Of the 10 groups of *Rhinolophus* now dealt with, only two, *R. philippinensis* and *R. simplex*, are native to the regions east of Wallace's Line, the first occurring in the Philippines, Celebes, and the Moluccas, the second in the Moluccas, New Guinea, and Australia. Additional examples of local specialization are seen in *Hipposideros*, two groups out of the six known in the Indo-Australian region having New Guinea-Australian patterns of distribution. Two genera derived from *Hipposideros*, namely, *Anthops* and *Rhinonycteris*, are also New Guinea-Australian. The total number of instances of evolutionary development probably of Australian origin amounts to 35. Many of these, as are many of the species groups of *Pteropus*, some of the Macroglossinae, *Rhinolophus*, and *Hipposideros*, are comparatively recent. Others, such as *Dobsonia*, *Nyctimene*, *Notopteris*, *Chalinolobus*, *Scoteinus*, *Nyctophilus*, *Hipposideros muscinus*, *Anthops*, and *Rhinonycteris*, are probably older.

This last suggestion must be taken with some degree of reservation, because ample evidence exists to show that as long ago as Middle Eocene time certain genera, such as *Rhinolophus*, *Hipposideros*, and *Myotis* of the Microchiroptera, had become substantially as they are today. At that early period, there were still in existence vespertilinoid bats in which obsolescence of the claw of the index finger (present in most Megachiroptera) had not begun. Evolution in the Megachiroptera, contrary to that in the Microchiroptera, may have advanced relatively slowly until the Middle Oligocene, the horizon of the only known fossil fruit bat. That animal, *Archaeopterus transiens*, though as large as *Pteropus*, had the tail unshortened like that of *Notopteris*. The head and teeth in the specimen shown in Meschinelli's original plate cannot be clearly seen. Simpson (1944), demonstrating changes of rate in evolution, has pointed out that the major dental evolution of the horses took place rapidly in the Miocene, and he has adduced much more evidence to show that evolution is far from being a uniformly continuous process. We may also infer varying rates of development in the several families of bats.

THREE CHIROPTERAN FAUNAS

The bat fauna of the East Indies, weakly partitioned into a widespread element and a restricted one, can instead be divided regionally into three major faunas and many minor geographical subfaunas. For convenient analysis, I have placed symbols at the left of each list to indicate the various types of distributional patterns; the following letters are employed to provide a shorthand expression of the assumed region of origin of each:

A Asia
Z Intercontinental, chiefly Old Asiatic of Philippines, Celebes, Lesser Sundas, Moluccas
N New Guinea-Australia-Solomon Islands
O Oceania, comprising waifs from other faunas

It must be admitted that the evidence favoring establishment of these "faunas" is rather frail. If both morphological and geographical isolation is discernible, the species or "group" under consideration is treated as having originated in its present general environment. Borderline cases occur in which a moderate degree of morphological distinction is combined with a very extensive geographical range, e.g., in the *Pteropus hypomelanus* group. In that group, which spreads between Malaysia and Oceania, the intercontinental island area at the center is arbitrarily chosen as the original habitat, even though the Greater Sunda region is almost equally probable.

A. Asiatic and Malaysian Bats

With few exceptions, the following geographical groups appear to have an Asiatic (usually a Malaysian) center of distribution. An exception is the *Pteropus vampyrus* group, which could easily have evolved beyond the continental borders, as did most other species groups of *Pteropus*, but is today located principally west of Wallace's Line. The many Indian and Malayan species that do not reach Wallace's Line are omitted from this present work.

A.1. Asiatic and Malayan Bats reaching but not crossing Wallace's Line[1]:

Cynopterus sphinx (to India)[2]
Cynopterus (*Niadius*) (Malay)
Balionycteris maculata (Malay), *seimundi* (Borneo)
Macroglossus minimus (Malay)
Pipistrellus abramus (to Japan)
Pipistrellus circumdatus (to Burma)
Pipistrellus joffrei group (to Burma)
Nycteris javanica (*Nycteris* to Africa)
Hipposideros speoris group (to Africa)
Harpiocephalus harpia (India)
Chaerephon plicatus (Malay and Africa)
Rhinolophus affinis group (Malay)
Rhinolophus lepidus group (India-China)
Rhinolophus trifoliatus group (India)
Rhinolophus luctus group (India, China)

Some members of this section are wide ranging, with representatives in India and Africa. Those in the subgroups that follow show a greater degree of endemism.

A.2. Java (endemic):

Chironax melanocephala, derived from *Cynopterus*

A.3. Borneo (endemic):

Dyacopterus spadiceus, derived from *Cynopterus*
Penthetor lucasi, derived from *Cynopterus*
Hesperoptenus doriae

A substantial number of species groups, apparently of Asiatic origin, have transgressed the continental shelf area, reaching all or certain of the Intercontinental islands or even beyond. They form a number of individual distributive patterns.

A.4. Malaysia to the Lesser Sunda Islands:

Taphozous longimanus

A.5. Asia through the Lesser Sunda Islands to Moluccas:

Murina, various races (to India, Siberia)
Kerivoula picta (to South China)

A.6. Greater Sundas (omitting Lesser Sundas?), Moluccas:

Glischopus, various races, pipistrelloid

A.7. Malaysia (omitting Celebes, Lesser Sundas), New Guinea:

Kerivoula pusilla group (Malay)

A.8. Asia to Wallace's Line, and the Philippines:

Megaerops ecaudatus (Malay), *wetmorei*[3] (Philippines)
Chaeromeles (Malay)
Eonycteris spelaea (to Malay)

[1] Except *Rhinolophus affinis* group, which reached Lombok.
[2] Extent of northern and western ranges placed after names in parentheses.
[3] Possibly not a *Megaerops*.

Rhinolophus macrotis group (to India)
Scotophilus temminckii (to India)
Kerivoula papillosa (Malay Peninsula)
Taphozous melanopogon (Malay)
Tylonycteris pachypus (to Malay)
Coelops frithii (to Burma)

A.9. Malaysia to Philippines and Lesser Sunda Islands:

Pteropus vampyrus group (to Malay)
Kerivoula hardwickii (to Burma)

A.10. Malaysia to Celebes:

Pipistrellus affinis group (to Burma)
Tylonycteris robustulus (to Burma)
Scotophilus heathii (to India and China)

A.11. Asia to Philippines and Celebes:

Cynopterus brachyotis (to India)
Myotis (*Chrysopteron*) (to Africa)
Mops, including *M. sarasinorum* and *Philippinopterus lanei* (to Africa)
Emballonura monticola (to Malay)
Rhinolophus borneensis group (to Malay)
Rhinolophus arcuatus group (to Malay)

A.12. Asia to Philippines, Celebes, and Moluccas:

Rousettus leschenaulti (to India)
Megaderma spasma (to India)

A.13. Malaysia, also Moluccas, New Guinea, Solomons:

Aselliscus (a Malaysian species and a Papuan species)

A.14. Asia to Philippines, Moluccas, Australia:

Myotis (*Selysius*) (to Europe)
Myotis (*Leuconoë*) (to Europe)

A.15. Moluccas (endemic):

Thoöpterus nigrescens, derived from *Rousettus*

A.16. Asia to Philippines, New Guinea, Solomons, Australia:

Pipistrellus coromandra group (to India)
Miniopterus schreibersii (to Europe)

A.17. Asia to all tropical East Indies excluding Australia and Oceania:

Rousettus amplexicaudatus (to India)
Pipistrellus tenuis group (Malay)
Hipposideros bicolor (to India)
Hipposideros galeritus (to Malay)
Hipposideros diadema (to Malay)

A.18. Asia, through islands generally, to Oceania:

Pteropus hypomelanus group (to Malay)

N. New Guinea-Australian Bats

A substantial bat fauna has accomplished the latter phases of its evolution on the Australian continental mass. Elements of it have spread beyond the Australian continental shelves to the Solomon Islands, to some of the Intercontinental islands, and occasionally to Oceania. Bats belonging to this fauna are designated N (= New Guinea-Australia).

N.1. Australia (with Tasmania)-New Guinea-Solomon Islands:

Pteropus macrotis group (to north Australia)
Pteropus scapulatus group (to north Australia)
Pipistrellus tasmaniensis (Victoria, Tasmania only)
Pipistrellus regulus (Western Australia only)
Syconycteris australis (to northern Australia)
Eptesicus pumilus group
Scoteinus (Australian section)
Chaerephon (Australian section)
Saccolaimus flaviventris
Taphozous australis, etc.
Rhinonycteris aurantiaca (to northern Australia)
Rhinolophusmeg aphyllus (Australia only)
Hipposideros muscinus group (to northern Australia)
Macroderma gigas (to northern Australia)
Nyctophilus (also doubtfully in Timor)

N.2. Australia-New Guinea, etc., reaching Oceania:

Pteropus conspicillatus, including *geddiei*
Chalinolobus, several species

N.3. New Guinea (endemic):

Dobsonia minor
Paranyctimene raptor
Philetor rohui

N.4. Solomon Islands (endemic):

Pteralopex atrata, anceps, derived from *Pteropus*
Nesonycteris woodfordi, macroglossine
Anamygdon, derived from *Kerivoula?*
Anthops ornatus, hipposiderine

N.5. New Guinea and Solomons:

Pteropus neohibernicus
Melonycteris melanops, macroglossine

N.6. Moluccas-New Guinea and Solomons:

Pteropus rayneri group
Dobsonia viridis group
Syconycteris crassa, macroglossine
Emballonura raffrayana group
Mormopterus (also tropical America)

N.7. Lesser Sundas-northern Australia and New Guinea:

Rhinolophus simplex

N.8. Philippines, New Guinea, and Solomons:

Rhinolophus calcaratus[1]

N.9. Celebes, Moluccas, New Guinea, Solomon Islands:

Emballonura (Mosia)

N.10. Lesser Sundas, Moluccas, New Guinea:

Pteropus melanopogon group

Z. Bats of Intercontinental Island Groups

A series of bat genera and of species groups, indicated by the letter Z, almost all basically of Asiatic origin, is endemic to, or originates in, the Intercontinental island groups. Those island groups are normally separated into four faunal subdivisions: Philippines, Celebes, Moluccas, Lesser Sundas. To a limited extent endemism appears in each of those subdivisions.

Five of the examples of speciation in the region are Philippine, four are Celebean, one is Moluccan. In addition, 11 species have invaded from New Guinea, four originated in the Solomon Islands, and nine are now widely dispersed through the various islands.

The bat fauna of this region is also divisible into a larger northern group of genera, found in the Philippines and Celebes, with colonizers spreading to other islands; and a smaller, southern group, concentrated in the Lesser Sunda Islands, the Moluccas, and Celebes. The latter is more closely related to the New Guinea-Australian fauna; it tends to spread to the east and west, though but little to the north. In any case, the precise geographical patterns of Z species and species groups are much varied. The first or northern group comprises the sections Z.1–Z.9; the second or southern group, Z.10–Z.15.

Z.1. Philippine Islands (endemic):

Saccolaimus pluto
Megaerops ecaudatus, derived from *Cynopterus*
Ptenochirus jagori, derived from *Cynopterus*

Z.2. Philippines to Oceania:

Pteropus mariannus group
Pteropus pselephon group

Z.3. Celebes (endemic):

Boneia bidens, derived from *Rousettus*
Styloctenium wallacei, derived from *Pteropus*
Eonycteris rosenbergi (Malay)
Pipistrellus minahassae

Z.4. Philippines and Celebes:

Acerodon[2] *jubatus, celebensis,* derived from *Pteropus*
Harpionycteris whiteheadi, celebensis (endemic subfamily)

Z.5. Philippines, Celebes, Moluccas:

Rhinolophus philippinensis group

Z.6. Borneo, Philippines, Celebes, Lesser Sundas, New Guinea, Australia:

[1] Philippine relationship not well established.

[2] Recorded by Mertens from Flores and Sumbawa.

Macroglossus lagochilus

Z.7. Philippines, Celebes, Moluccas, New Guinea, Solomons:

Pteropus temmincki group

Z.8. India, Philippines, Lesser Sundas, New Guinea, Australia, Oceania:

Miniopterus australis

Z.9. Philippines and New Guinea to Oceania:

Miniopterus tristis

Z.10. Celebes, Moluccas, New Guinea, Australia:

Nyctimene papuanus (perhaps fundamentally of New Guinea-Australian origin)

Z.11. Celebes, Lesser Sundas, Moluccas, New Guinea, Solomons, Australia (north):

Nyctimene cephalotes (perhaps fundamentally of New Guinea-Australian origin)

Z.12. Lesser Sundas:

Dobsonia peronii (probably of New Guinea-Australian origin)

Z.13. Celebes, Moluccas, and Lesser Sundas:

Rhinolophus euryotis group

Z.14. Java, Celebes, Lesser Sundas, New Guinea:

Phoniscus, various species, near *Kerivoula*

Z.15. Bawean Island, Celebes, Lesser Sundas, south New Guinea, north Australia:

Pteropus alecto group

OBSERVATIONS AND CONCLUSIONS

Of 124 bat entities treated as Australasian, 54, or 44 per cent, are considered of Recent Asiatic origin, 36, or 25 per cent, of Australian origin, 22, or 18 per cent, of Intercontinental origin, two, *Notopteris* and *Mystacops*, of unknown origin, and the remainder are so widely distributed that it is not possible to assign them restricted places of origin.

A few Australian species groups, or even genera, have been represented in tables 1 and 2 by single items. They include *Chalinolobus* with four species, *Scoteinus* containing two species groups, *Chaerephon* with two species, and *Nyctophilus* and *Pharotis* totaling five species. The effect of listing these species and groups separately would be to raise the numbers of endemic Australian Microchiroptera even higher than appears in figure 1. It would increase the total number of Indo-Australian entities from 124 to 133 and the number of Australian or N species groups from 36 to 45; also it would alter percentage comparisons to show larger Australian components. Apart from this, such telescoping of the N fauna forestalls possible criticism to the effect that inadvertently more weight has been given Australian than Asiatic species. Moreover, the telescoping has not materially altered either the tenor of the paper or my conclusions.

Both the distinctively Australian fauna and the distinctively Intercontinental fauna are believed to have developed during relatively long periods of time from ancestry of ancient Asiatic (or geographically more remote) origin.

The numbers of species groups of the Australasian fruit bats and insectivorous bats are, respectively, 49 and 75 (= 124). A far smaller percentage of the former (30 per cent) than of the latter (65 per cent) have their distributional headquarters on the Asiatic mainland or in the Greater Sunda Islands. Conversely, a larger proportion of the fruit bats (50 per cent) than of insectivorous bats (43 per cent) have their geographical centers east of Wallace's Line. The figures at the end of table 1 show a progressive increase in the proportion of Megachiroptera to Microchiroptera eastward, up to about 50:50 in Celebes, Moluccas, and New Guinea. The rise in

the numbers of Microchiroptera in Australia is attributed to the presence there of a substantial group of relict microchiropteran genera. The small number of genera in "Sanghir, Talaut" is partly explained by imperfect recording. In the New Guinea-Australian continental area, including the Solomon Islands, the total proportion of all fruit bats to all insectivorous bats is as 22 to 38. But if the indigenous groups alone of the region are considered the picture is reversed; there are 17 indigenous fruit bats and only 20 indigenous insectivorous bats. This perhaps shows that the latter had relatively greater migratory ability during recent geological periods.

The 54 Asiatic or A bats are dispersed as follows: 15 species groups (seven of them Megachiroptera) reach but do not cross Wallace's Line: 36 groups transgress it to the eastward to varying extents; only 15 of the groups continue to the east of modified Weber's Line.

In a westerly or northerly direction, four only of the Asiatic bat groups are restricted to the Greater Sunda Islands, 36 extend to India, China, or both, and a few others have much greater ranges.

Many of the species groups of Asiatic and Malayan origin that invaded the islands from the west eastward are recorded only on certain of the islands. Some have penetrated only to the Philippines: *Eonycteris spelaea, Tylonycteris pachypus, Scotophilus temminckii, Kerivoula papillosa, Cheiromeles, Taphozous melanopogon, Rhinolophus macrotis,* and *Coelops.* A few species groups have reached only Celebes: *Pipistrellus affinis, Tylonycteris robustulus, Scotophilus heathii.* Others have extended along the Lesser Sundas to the Moluccas (*Murina* and *Nycteris*[1]) and New Guinea (*Kerivoula* and *Phoniscus*).

In the case of most members of the Asiatic group, invasion has been more widespread, e.g., *Rousettus* reaches the Intercontinental islands, northern New Guinea, and the Solomons, yet the *Cynopterus* group of genera, except *Thoöpterus,* endemic to the Moluccas, is not found beyond the Philippines and Celebes. The two subgenera of *Myotis, Selysius* and *Leuconoë,* both reach the Philippines, the Moluccas, and Australia; the *Pipistrellus coromandra* group reaches the Philippines and the northern part of the Australian continental area. Other generally dispersed Asiatic species groups include the widely ranging *Miniopterus schreibersii* group; *Megaderma* and *Murina,* reaching the Moluccas; *Taphozous* with *Saccolaimus,* regarded generically, found from Africa to Australia; the *Hipposideros bicolor* and *H. galeritus* groups, of which the sources remain undetermined. Seen on a world scale, the representatives of ancient, extremely wide-ranging families, subfamilies, or generic groups comprise *Rousettus, Pipistrellus, Eptesicus, Scoteinus,* the Kerivoulinae, the Molossidae (*Chaerephon*), the Emballonuridae with many relatives in tropical America, the Megadermidae, the Rhinolophinae, and the Hipposiderinae.

Among the 38 species groups treated as of New Guinea-Australian or N origin, three are endemics of New Guinea and four endemics of the Solomon Islands. The *Pipistrellus tasmaniensis* group occurs only in southeastern Australia and Tasmania. The origin and relationships of the New Guinea-Australian fauna, including the Solomon Islands, are remote geographically, and its arrival there must have taken place very long ago. There is no good clue, for instance, to the origins of such distinctive genera as *Dobsonia, Nyctimene,* or the Oceanic *Notopteris* and *Mystacops. Chalinolobus* is most nearly related to *Glauconycteris* of Africa, *Nyctophilus* to *Antrozous* of western North America, and *Mormopterus,* doubtfully, to the *"Mormopterus"* of tropical America.

The bat fauna of New Guinea, numbering 37 species groups, contrary to the case in the rodents and marsupials, contains only three endemic species: *Dobsonia minor, Paranyctimene raptor,* and *Philetor rohui.* The number of N species in New Guinea is 27 (16 Megachiroptera).

The Solomon Islands, most nearly allied faunistically to New Guinea, contain a total of 29 species. Nineteen are N bats (12 Megachiroptera), of which four genera

[1] To Timor.

(three monotypic) are indigenous. Those four genera are derived from widely separated subfamilies: *Pteralopex*, with two weak species, from the Pteropinae, *Melonycteris* from the Macroglossinae, *Anamygdon* from the Kerivoulinae, and *Anthops* from the Hipposiderinae.

The few bats found in Oceania, meaning the more remote Pacific islands such as the Carolines, Fijis, Hawaii, New Caledonia, New Zealand, are drawn either from genera and species groups still found in the Philippines, New Guinea, and the Solomon Islands, or from much wider-ranging groups. The *Pteropus mariannus*, *P. pselaphon*, and *P. samoensis* groups are Intercontinental with strays reaching Oceania. The wide-ranging *P. hypomelanus* group has contributed several forms. The isolated *Notopteris* of Fiji, New Hebrides, and New Caledonia is an extremely distant morphological ally of *Macroglossus*. *Emballonura*, with several Australasian species, is represented by one species in the Carolines and a second in Fiji, Samoa, the Marshalls, and New Hebrides. *Miniopterus* is present also in the Loyalty Islands and New Caledonia. The Australian *Chalinolobus* occurs in New Caledonia, New Hebrides, and New Zealand. *Mystacops* is known only from New Zealand. *Lasiurus semotus* of Hawaii is the only Oceania bat that originally came from America.

The Intercontinental region, comprising the several groups of islands lying between the Asiatic and Australian continental shelves, contains a total of 63 species groups, of which 22 are regarded as old Asiatic (nine being endemic Megachiroptera, one the endemic subfamily Harpionycterinae containing only *Harpionycteris*, and two endemic species of the microchiropteran genera *Pipistrellus* and *Taphozous*). That regional fauna is perhaps best characterized by the many distinct groups of *Pteropus* and by the two generic offshoots of *Pteropus*, *Acerodon*, and *Styloctenium*. Only the *Pteropus vampyrus* group is here classed as Asiatic rather than Intercontinental, although several of the other groups of *Pteropus* are distinctively Australian. The Macroglossinae are moderately developed in the Intercontinental area but show rather more diversification in New Guinea-Australia. The low endemism in the Microchiroptera is noteworthy.

Of all the Z and N species of the Intercontinental and New Guinea-Australian areas, only two Megachiroptera cross to the west of Wallace's Line. Yet no fewer than 12 of the Megachiroptera and seven Microchiroptera occur on islands immediately adjoining it. This may be compared with the seven Megachiroptera and eight Microchiroptera that reach but do not cross the "Line" from the west.

The Intercontinental island region or Z area contains more indigenous Megachiroptera than indigenous Microchiroptera. Of the 31 species groups of fruit bats present, 15, or nearly 50 per cent, are believed to have had secondary origin there, while among the 45 groups of insectivorous bats only eight, or 18 per cent, come under that category. These figures suggest that the fruit bats have been established in the East Indies longer or with greater facility than the insectivorous bats. Disparity between the pictures presented by the fruit bats and the insectivorous bats may be partly explained by imperfect collecting.

A small but substantial part of the Intercontinental fauna is formed by a New Guinea-Australian element of 14 species, nine of them Megachiroptera. Three of these even reach the Greater Sunda Islands. One, the *Hipposideros calcaratus* group, may be represented also in the Philippines, although that relationship is not clearly proved.

The Philippine chiropteran fauna of 42 species groups is primarily Asiatic. It has five modern Asiatic Megachiroptera and 18 modern Asiatic Microchiroptera. There is an Intercontinental (old Asiatic) element totaling nine Megachiroptera (three endemic) and five Microchiroptera. The remainder are unclassified. The Carolines have been reached by two Megachiroptera of Philippine origin.

Celebes, with 33 recorded[1] species groups, 15 of them megachiropteran, has

[1] Nine more Microchiroptera will probably be discovered.

four endemics. Several of the important groups are present also in the Philippines. A proportion of the species is concentrated along the Lesser Sundas-Australian latitudes, and a number of Papuan species occur. Thirteen extremely wide-ranging Asiatic species form a substantial proportion of the bat fauna.

The Moluccas, deep-sea islands very near New Guinea, have drawn their Chiroptera in about equal proportions from Celebes and Papua. They mark the eastern limit of *Rousettus leschenaulti*, *Glischropus*, *Murina*, *Kerivoula picta*, and *Megaderma spasma*. A relationship, via northern New Guinea, with the Bismarcks is exemplified by the distributional patterns of *Rousettus amplexicaudatus*, the *Pteropus rayneri* and *P. temmincki* groups, and *Dobsonia viridis*. The total number of species groups is 32, of which 13 are New Guinea-Australian, nine are Z bats, and nine others are widespread Asiatics. *Thoöpterus nigrescens* is the only endemic.

The Lesser Sunda Islands have a relatively poor bat population of nine Megachiroptera and nine Microchiroptera. The *Pteropus alecto* group, found from Australia to Bawean and northward as far as north Celebes, is a species that may well have originated there. Papuan and Celebes elements and the widely dispersed Asiatic species occur. More collections are needed.

Mayr's "line of 50:50 balance" (1944a, pp. 11–12), the hypothetical line at which the number of Asiatic and Australian species are the same, shows nearly the same results as in the case of the birds when applied to the Chiroptera. Mayr was able to assign all the Intercontinental species of birds to either an Asiatic or an Australian origin. He then found that the line where the avian fauna was composed of 50 per cent Asiatic and 50 per cent Australian species ran approximately through the Molucca Strait, or nearly in the position of the original Weber's Line. In order to study the distribution of the bats in relation to the several water gaps between Celebes and Australia, I have prepared a list of species groups (table 2) from which all non-pertinent species have been omitted. The line of chiropteran balance passes somewhat farther east than that of the birds, or between the Moluccas and New Guinea, as shown in figure 1. This conclusion is partly presumptive, and therefore weakened, from the fact that several of the very wide-ranging species groups, though known both from Celebes and New Guinea, have been merely postulated as also occurring in the Moluccas. Also more indigenous species may exist. Again, the position of the line of balance differs according to whether the Megachiroptera or the Microchiroptera are considered; in the Moluccas the former have only a moderately high percentage of Asiatic species groups (modern Asiatic plus Intercontinental or old Asiatic), while the Microchiroptera include three times as many Asiatic and Australian species groups. The balance in the Megachiroptera falls exactly at the Moluccas; in the Microchiroptera it is more nearly in New Guinea.

The rate of fall in numbers of New Guinea-Australian species groups westward is less rapid in the Megachiroptera than in the Microchiroptera. This is probably explainable by the exclusively tropical habitats, perhaps related to constantly available supplies of fruit, occupied by the Megachiroptera in contrast to both the tropical and low subtropical habitats of the Microchiroptera; those Microchiroptera that live at colder elevations are less likely to be able to colonize successfully in the tropical zones than are the lowlands species.

The flat curves that appear both for the old and the recent Megachiroptera and Microchiroptera (fig. 2) indicate more generalized dispersal than the steep curve of the recent Microchiroptera, which suggests a recent wave of invasion perhaps still operative. The greater number of old than recent Megachiroptera and the absence of any recent species of that suborder in Australia indicate thorough establishment of the old groups (with generic endemism developed in Celebes and the Moluccas) and but little invasion in recent times. This interpretation is necessarily strongly subjective. For instance, one or more of the three species treated by me as

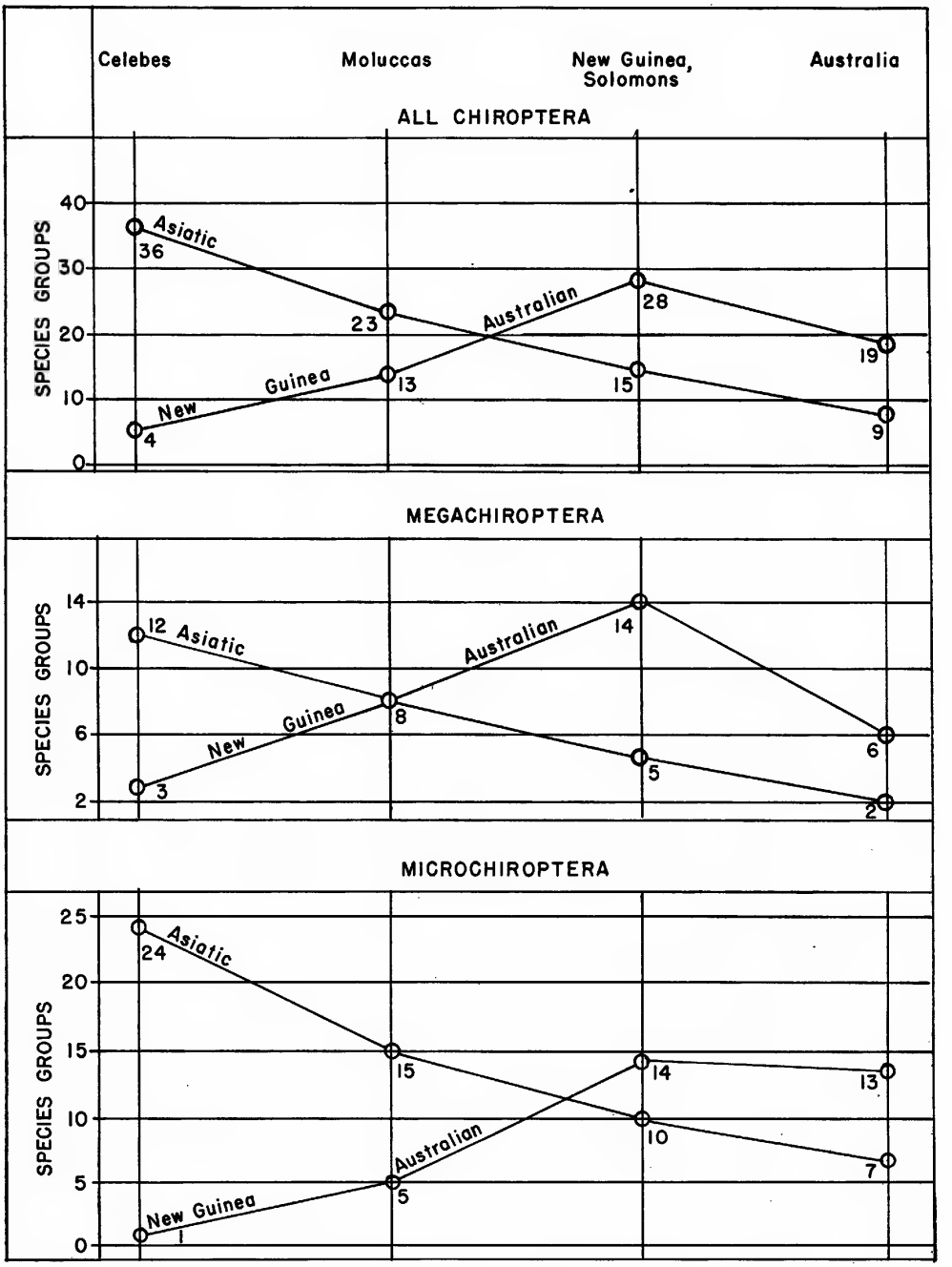

Fig. 1. Numbers of species groups respectively of Asiatic and Australian origin in relation to Mayr's "line of 50:50 balance."

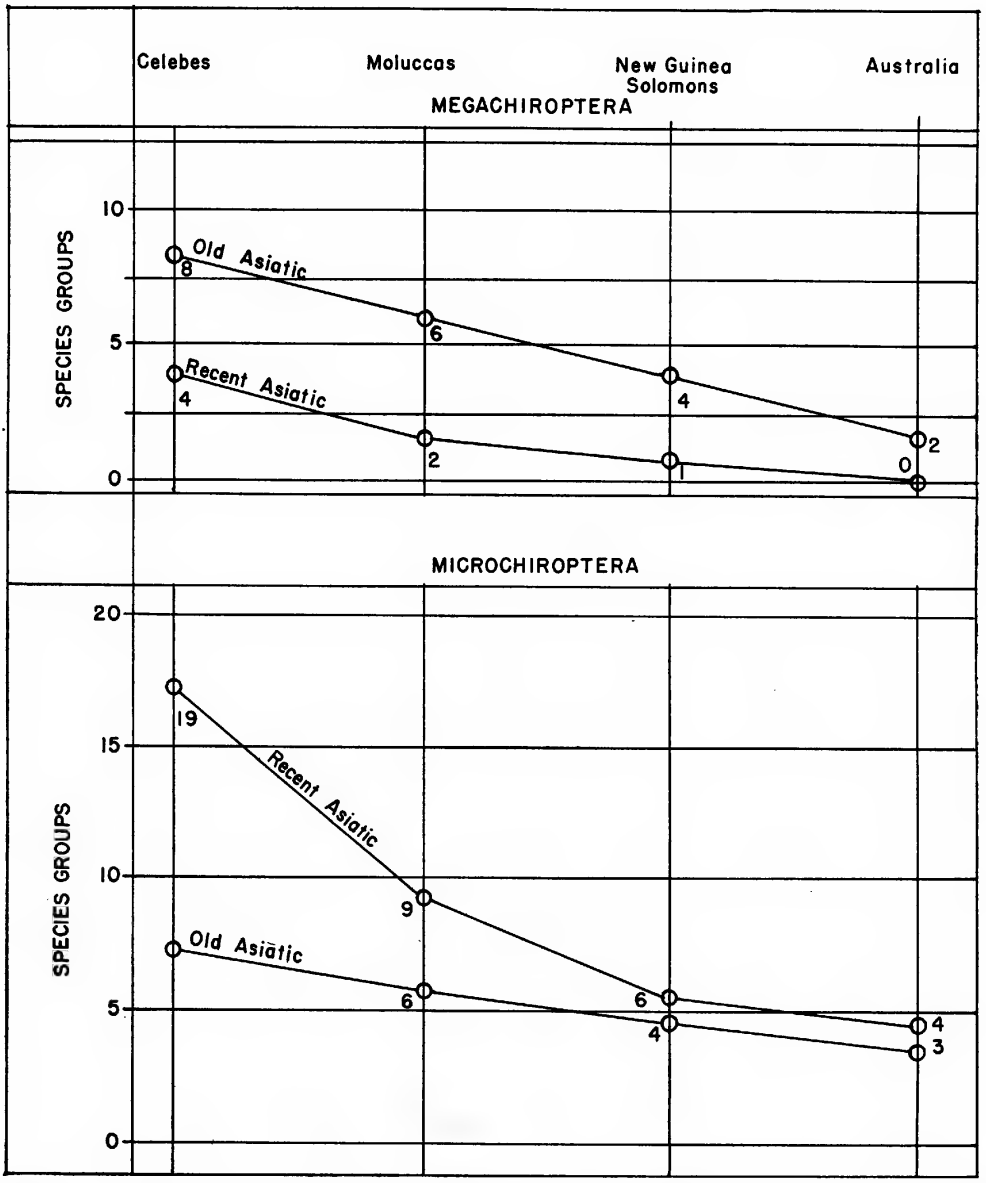

Fig. 2. Species groups of old and Recent Asiatic bats between Celebes and Australia, to show the relatively great dispersive activity of the Recent Microchiroptera compared with the stability of the Megachiroptera.

old Asiatic Microchiroptera reaching Australia may be regarded by others as truly Australian or N bats.

No interpretation of Wallace's Line other than that offered by Mayr (1944a) and foreshadowed by many other writers is indicated by the distributional patterns of the Chiroptera. The concentration of 15 species groups along the margin of the old Asiatic continent requires no special explanation; it shows merely that, as is the case with many of the birds and butterflies, a limited number of winged mammals have failed as yet to cross a rather narrow water barrier. The ancestors of the three faunas indicated in this paper did not reach the

Intercontinental island groups or Australia as faunal groups. It is far more probable that single species came one by one as waifs from the Asiatic mainland through immense periods of time. It was only after sufficient numbers of species had become established in Australia or on the several groups of Intercontinental islands that those areas become important as secondary points of dispersal. Thus, the Sahul Shelf, which is the edge of continental Australia and close to modified Weber's Line, bears the same general relationship to Australia-New Guinea that modified Wallace's Line, near the continental shelf of Asia, bears to the present Asiatic mainland. Each continental center has acted as a faunal reservoir from which species drifted out continuously onto the islands.

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TABLE 1

COMPLETE LIST OF THE CHIROPTERAN SPECIES GROUPS OR UNITS OF HIGHER RANK UPON WHICH THIS PAPER IS BASED

All footnotes on page 19.

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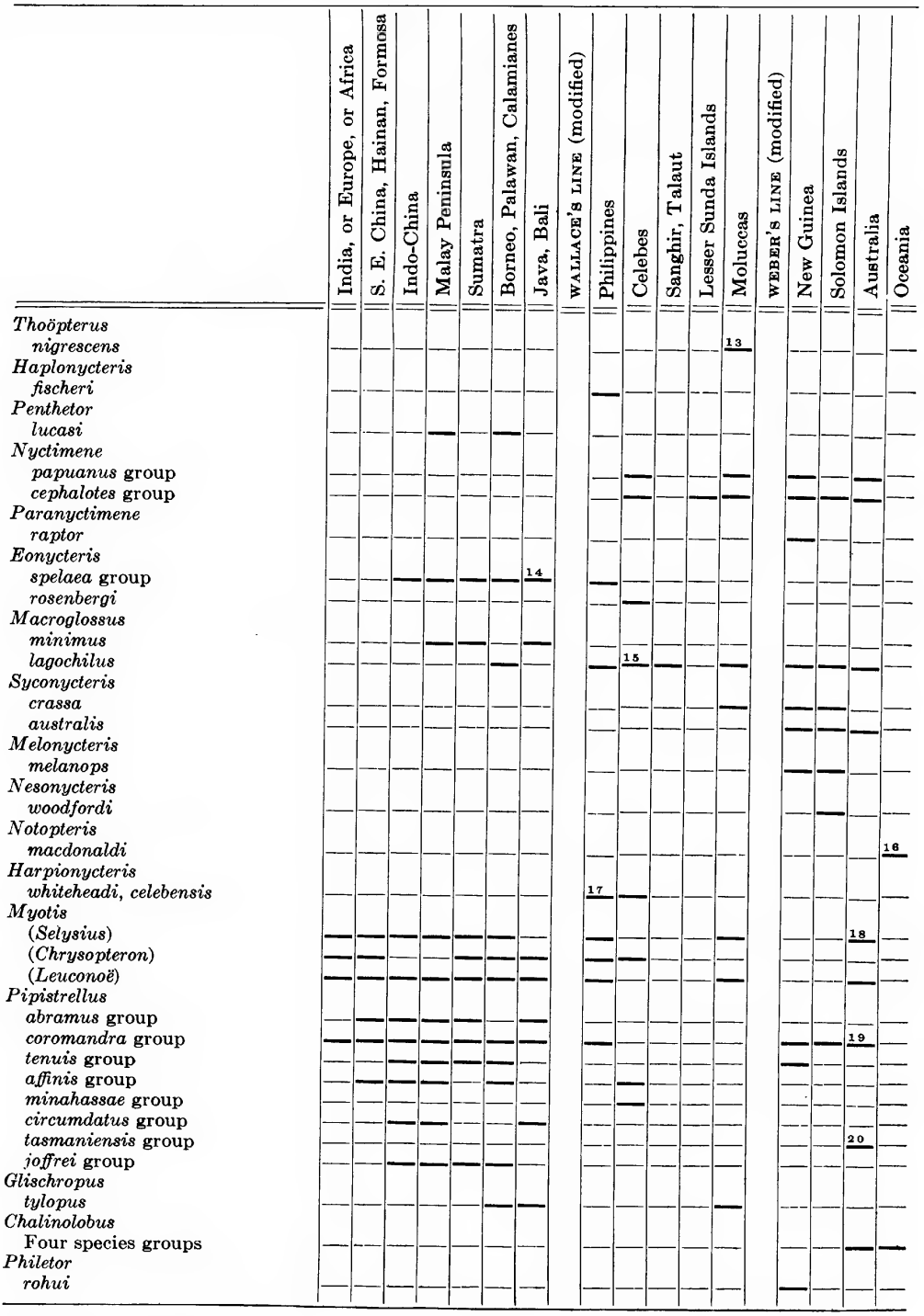

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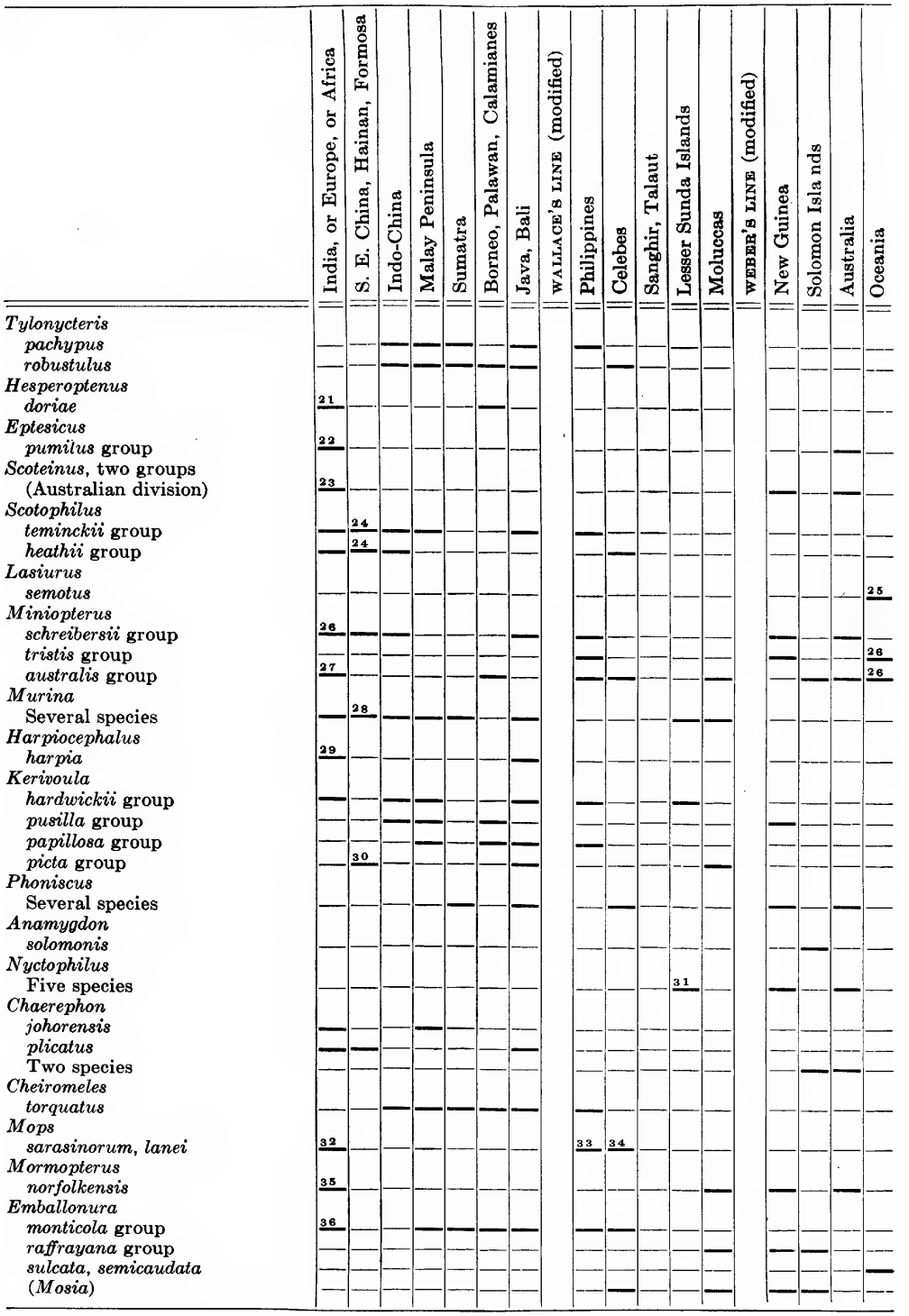

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TABLE 1

COMPLETE LIST OF THE CHIROPTERAN SPECIES GROUPS OR UNITS OF HIGHER RANK UPON WHICH THIS PAPER IS BASED—(*Continued*)

	India, or Europe, or Africa	S. E. China, Hainan, Formosa	Indo-China	Malay Peninsula	Sumatra	Borneo, Palawan, Calamianes	Java, Bali	WALLACE'S LINE (modified)	Philippines	Celebes	Sanghir, Talaut	Lesser Sunda Islands	Moluccas	WEBER'S LINE (modified)	New Guinea	Solomon Islands	Australia	Oceania
Taphozous																		
longimanus	[37]			—		—	—					—						
melanopogon		—	—	—	—		—		—									
australis, fumosus															—		—	
Saccolaimus																		
saccolaimus						—	—											
pluto									—									
flaviventris, etc.																—	—	
Megaderma																		
spasma	—		—	—	—	—	—		—	—			—					
Macroderma																		
gigas																	—	
Nycteris																		
javanica	—			—		—	—					[38]						
Rhinolophus																		
simplex group												—	—		—		—	
borneënsis group				—		—	—		—	—								
affinis group	[39]			—		—	—					[40]						
lepidus group	[39]	—	—	—	—		—											
arcuatus group				—	—		—		—	[41]								
euryotis group										[41]		—	—					
philippinensis									—	—			—					
macrotis	[39]								—									
trifoliatus section				—	—		—											
luctus section	[39]	—	—	—		—	—											
megaphyllus group																	—	
Hipposideros																		
bicolor group	[39]								—						—	—	—	
calcaratus group									[42]						—			
galeritus group	[39]			—	—	—	—		—		—		—		—	—	—	
diadema section	[39]			—	—	—	—		—	—		—	—		—	—	—	
speoris group	—	—	—	—	—	—	—											
muscinus group[43]															—		—	
Anthops																		
ornatus																—		
Aselliscus																		
Two species			—	—									—		—	—		
Rhinonycteris																		
aurantiaca																	—	
Coelops																		
frithii		—	—	—	—	—	—		—									
Mystacops																		
tuberculata																		—
Total numbers of strongly defined species groups, actually recorded,[44] of:																		
Megachiroptera	2	4	7	12	9	11	11		15	15	5	9	15		20	16	10	5
Microchiroptera	29	19	27	34	25	26	35		27	18	1	9	17		20	13	23	6
GRAND TOTAL	31	23	34	46	34	37	46		42	33	6	18	32		40	29	33	11

All footnotes on page 19.

FOOTNOTES TO TABLE 1

[1] Northern side.
[2] Long-faced.
[3] Approximately = *Sericonycteris* Matschie.
[4] Formosa only.
[5] *P. pumilus.*
[6] Also on Buru Island.
[7] Short-faced.
[8] *P. tablasi.*
[9] Lombok and Timor.
[10] Also *P. aterrimus* on Kangean Island.
[11] *M. wetmorei.*
[12] *B. seimundi.*
[13] Morotai Island.
[14] Specimens in Archbold collection.
[15] And Buru Island.
[16] And *N. neocaledonica.*
[17] Mindoro only.
[18] *M. australis* aberrant.
[19] *P. regulus* in Western Australia.
[20] Tasmania, New South Wales.
[21] Other species referred to *Hesperoptenus.*
[22] Some African *Eptesicus* closely related to Australian.
[23] Relationship doubtful.
[24] Both Hainan Island.
[25] Hawaii.
[26] Europe and Africa.
[27] Also in India.
[28] North to Manchuria.
[29] Headquarters in India and Burma.
[30] Hainan.
[31] Doubtfully in Timor.
[32] India and Africa.
[33] *Philippinopterus.*
[34] *M. sarasinorum.*
[35] *Mormopterus* in tropical America and Madagascar.
[36] *Emballonura* in Madagascar.
[37] *Taphozous* in Africa.
[38] Doubtfully Timor.
[39] India.
[40] Lombok, eastern limit.
[41] Buru Island.
[42] Doubtfully related.
[43] Possible relationship to *H. cyclops* group of Africa.
[44] In the Intercontinental area a number of species not yet recorded will undoubtedly be found.

TABLE 2

SEVENTY-THREE CHIROPTERAN SPECIES GROUPS (OR CATEGORIES OF HIGHER RANK) IN AREAS ADJOINING THE MOLUCCA STRAIT, THE HALMAHERA PASSAGE, AND THE TORRES STRAIT

	Probable Origin[1]	Macassar Strait	Celebes	Moluccа Strait	Moluccas Islands	Strait	New Guinea, Solomons	Torres Strait	Australia
Rousettus leschenaulti group	A	[2]→	—	→	—				
Rousettus amplexicaudatus group	A	→	—	→	—	→	—		
Boneia bidens	Z		[3]•						
Pteropus hypomelanus group	Z	←	—		—	→	—		
Pteropus conspicillatus	N				—	←	—	→	—
Pteropus caniceps group	Z		—		—				
Pteropus melanopogon group	N				—	←	—		
Pteropus rayneri group	N				—	←	—		
Pteropus temmincki group	Z		—		—	→	—		
Pteropus alecto group	Z		—		?[4]		—	→	—
Pteropus neohibernicus group	N						•		
Pteropus macrotis group	N						—	→	—
Pteropus scapulatus group	N						—	→	—
Acerodon celebensis group	Z		•						
Stylocteniun wallacei	Z		•						
Dobsonia minor	N						•		
Dobsonia exoleta, etc.	N		—	←	—	←	—		
Dobsonia viridis group	N				—	←	—		
Cynopterus brachyotis	A	→	—						
Thoöpterus nigrescens	Z				•				
Nyctimene papuanus group	N		—	←	—		—	→	—
Nyctimene cephalotes group	N		—	←	—		—	→	—
Eonycteris rosenbergi	A	→	—						
Macroglossus lagochilus	Z		—	←	—		—	→	—
Syconycteris crassa	N				—		—		
Syconycteris australis	N						—		—
Melonycteris melanops	N						•		
Harpionycteris celebensis	Z		•						
Myotis (*Selysius*)	A	→	—	→	—		?	→	—
Myotis (*Chrysopteron*)	A	→	—						
Myotis (*Leuconoë*)	A	→	?	→	—		?	→	—
Pipistrellus coromandra group	A	→	?	→	?	→	—	→	—
Pipistrellus tenuis group	A	→	?	→	?	→	—		
Pipistrellus affinis group	A	→	—						
Pipistrellus minahassae group	Z		•						
Glischropus tylopus	A	→	?	→	—				
Chalinolobus, four spp.	N								•
Philetor rohui	N						•		
Tylonycteris robustulus	A	→	—						
Eptesicus pumilus group	A								•
Scoteinus (Australian division)	N	→					—	←	•
Scotophilus heathii group	A	→	—						
Miniopterus schreibersii group	A	→	?		?	→	—	→	—
Miniopterus tristis group	Z	←	?		?		—		
Miniopterus australis group	Z	←	—		—		?	→	—
Murina	A	→	?	→	—				
Kerivoula pusilla group	A	→	?		?	→	—		
Kerivoula picta group	A	→	?	→	—				
Phoniscus, several species	Z	←	—		?		—	→	—
Anamygdon solomonis	N						•		
Nyctophilus, five species	N						—	←	—

All footnotes on page 21.

TABLE 2

SEVENTY-THREE CHIROPTERAN SPECIES GROUPS (OR CATEGORIES OF HIGHER RANK) IN AREAS ADJOINING THE MOLUCCA STRAIT, THE HALMAHERA PASSAGE, AND THE TORRES STRAIT—(*Continued*)

	Probable Origin[1]	Macassar Strait	Celebes	Molucca Strait	Moluccas Islands	Strait	New Guinea, Solomons	Torres Strait	Australia
Chaerephon, two species	N						—		—
Mops sarasinorum	A	→	—						
Mormopterus norfolkensis	N						—		—
Emballonura monticola group	A	→	—						
Emballonura raffrayana group	N				—	←	—		
Emballonura (*Mosia*)	N		—		—		—		
Taphozous australis, etc.	N						—		—
Saccolaimus flaviventris, etc.	N						—		—
Macroderma gigas	N								—•
Rhinolophus simplex group	N				—		—	→	—
Rhinolophus borneënsis group	A	→	—						
Rhinolophus arcuatus group	A	→	—						
Rhinolophus euryotis group	Z		—		—				
Rhinolophus philippinensis group	Z		—		—				
Rhinolophus megaphyllus group	N								—•
Hipposideros bicolor group	[5]		—		—		—	→	—
Hipposideros calcaratus group	N				—	←	—		
Hipposideros galeritus group	[5]	←	—		—		—	→	—
Hipposideros diadema group	Z	←	—		—		—	→	—
Hipposideros muscinus group	N						—		—
Aselliscus tricuspidatus	N				—	←	—		
Rhinonycteris aurantiaca	N								—•

[1] A, Asiatic; Z, Intercontinental or old Asiatic; N, New Guinea-Australian.
[2] Arrows indicate probable directions of dispersal.
[3] Dots mark endemic species.
[4] Interrogation marks indicate lack of record but also assumed presence.
[5] No limited region of origin is suggested.